PhytoKeys 263: 1–15 (2025)
DOI: 10.3897/phytokeys.263.163351

Research Article

# *Dryopteris pycnolepis*, a new fern species from northern Vietnam, with miscellaneous notes on *Dryopteris* sect. *Splendentes* (Dryopteridaceae)

Jun-Kai Huang[1,2], Xiao-Ji Li[1,2], Lian-Xuan Zhou[1], Zheng-Yu Zuo[3], Shi-Yong Dong[1]

1 *Key Laboratory of National Forestry and Grassland Administration on Plant Conservation and Utilization in Southern China, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou 510650, China*
2 *University of Chinese Academy of Science, Beijing 100049, China*
3 *Center for Interdisciplinary Biodiversity Research & College of Forestry, Shandong Agricultural University, Tai'an, 271018, China*
*Corresponding author: Shi-Yong Dong (dongshiyong@scib.ac.cn)*

## Abstract

A new woodfern species, *Dryopteris pycnolepis*, is described from northern Vietnam. The new species differs mainly in having broadly lanceolate scales (versus ovate-lanceolate) on the stipe and rachis, lateral pinnae with the basal acroscopic pinnules longer than their immediately adjacent pinnules (versus subequal), and fibrillose scales present on both surfaces of pinnules (versus glabrous). Phylogenetic analyses of plastome sequences support both the distinctness of *D. pycnolepis* as a species and its close affinity to *D. sikkimensis*. Morphological comparisons and phylogenetic analyses confirm that these two species, together with *D. rubrobrunnea* and *D. splendens*, form a small natural group (i.e., sect. *Splendentes*) within the *Dryopteris* clade of this genus. It appears to be a replacement species of the Sino-Himalayan *D. sikkimensis* in northern Vietnam. Section *Splendentes* is shown to be geographically restricted to the Sino-Himalaya region and northern Vietnam, excluding eastern Asian species previously included in this section. The discrepancy between phylogenetically and morphologically inferred interspecific relationships within sect. *Splendentes* is highlighted and briefly discussed. The correct authorship of the name *D. splendens* is noted to be "(Bedd.) Kuntze."

**Key words:** *Dryopteris splendens*, morphology, phylogeny, plastid genome, taxonomy

OPEN ACCESS

**Academic editor:** Blanca León
**Received:** 27 June 2025
**Accepted:** 12 August 2025
**Published:** 15 September 2025

**Citation:** Huang J-K, Li X-J, Zhou L-X, Zuo Z-Y, Dong S-Y (2025) *Dryopteris pycnolepis*, a new fern species from northern Vietnam, with miscellaneous notes on *Dryopteris* sect. *Splendentes* (Dryopteridaceae). PhytoKeys 263: 1–15. https://doi.org/10.3897/phytokeys.263.163351

**Copyright:** © Jun-Kai Huang et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

## Introduction

*Dryopteris* Adans., commonly known as woodferns, is one of the largest genera of ferns, consisting of ca. 348 species (excluding hybrids) (Hassler 1994–2025). This genus is widely distributed in temperate and montane tropical regions of the world, with its distribution center in the Sino-Himalaya region, including western China (SE Xizang, Yunnan, and Sichuan), the eastern Himalaya, and northern Burma (Fraser-Jenkins 1989). According to Fraser-Jenkins (1989), approximately 76 species of *Dryopteris* s. str., excluding species traditionally placed in *Acrophorus* C.Presl, *Acrorumohra* (H.Ito) H.Ito, *Diacalpe* Blume, *Dryopsis* Holttum & P.J.Edwards, *Nothoperanema* (Tagawa) Ching, *Peranema* D.Don, and *Stenolepia* Alderw., are present in this region. All these satellite genera

were phylogenetically resolved within *Dryopteris* (Zhang et al. 2012; Kuo et al. 2016) and thus were subsumed under *Dryopteris* taxonomically (PPG I 2016). The broadened *Dryopteris* has been shown to be a monophyletic genus, forming a sister relationship to *Arachniodes* Blume in Dryopteridaceae (Zhang et al. 2012; Zuo et al. 2025), with all sampled species resolved into 13 major clades (Zhang and Zhang 2012). Under the current monophyletic circumscription of *Dryopteris*, the Sino-Himalaya region (distribution center of the genus) harbors 204 species according to the database compiled by Hassler (1994–2025), representing approximately 60% of the species diversity of the whole genus. In contrast, species richness declines dramatically in southern regions adjacent to this center. For instance, only 30 species of *Dryopteris* are listed in Vietnam and 34 species in nearly the whole Indochina (including Thailand but excluding northern Myanmar) (Hassler 1994–2025).

During a botanical expedition to northern Vietnam in 2023, one of the authors (LXZ) collected three specimens of an unknown fern species (voucher number *16451*). The densely scaly, adaxially grooved frond axes and the discrete, round sori with round-reniform indusia indicate that the specimens represent a dryopteroid species. By reviewing the morphology of all described species of Dryopteridaceae in Vietnam and adjacent regions, we confirmed that the unknown species is morphologically most similar to *Dryopteris sikkimensis* (Bedd.) Kuntze, a very distinctive higher-Himalayan forest species (Fraser-Jenkins et al. 2018). *Dryopteris sikkimensis* has been considered closely related to *D. splendens* (Bedd.) Kuntze and *D. rubrobrunnea* W.M.Chu in the Sino-Himalaya region, which, together with a few eastern species, constitute sect. *Splendentes* Fraser-Jenkins under *Dryopteris* subg. *Dryopteris* (Fraser-Jenkins 1986, 1989; Fraser-Jenkins et al. 2018). To determine the identity of the unknown species from northern Vietnam, we conducted morphological comparisons and plastid sequence analyses between this unknown species and members of sect. *Splendentes*. The results are reported here.

## Methods

The morphological observation of the unknown species from northern Vietnam is based on herbarium specimens prepared (*LXZ 16451*, three fronds in five sheets) and deposited in the Herbarium of the South China Botanical Garden, Chinese Academy of Sciences (IBSC), as well as on living plants in the wild. Comparisons to species of *Dryopteris* sect. *Splendentes* (*D. rubrobrunnea*, *D. splendens*, and *D. sikkimensis*) are based on a thorough examination of specimens from 19 herbaria: B, BR, C, CDBI, E, GH, H, K, KUN, L, MICH, MO, NY, P, PE, S, US, TENN, and ZT. The spore morphology of the unknown species was examined using a JEOL JSM-IT210 scanning electron microscope at 15 kilovolts accelerating voltage in the public laboratory of the South China Botanical Garden, Chinese Academy of Sciences. Prior to observation, samples were sputter-coated with a 10 nm platinum layer using a SuPro Instruments Mini Coater.

To infer the systematic position of the unknown species within *Dryopteris*, we performed sequencing and phylogenetic analysis of the whole plastome. Our sampling strategy included representatives of *Dryopteris* sect. *Splendentes* from the Sino-Himalaya region, species related to this section as indicated by previous phylogenetic studies (e.g., Zhang et al. 2012; Kuo et al. 2024; Zuo et

al. 2025), and some species collected from Guangdong, southern China, with two to four samples per species to assess intraspecific plastome divergence. The final dataset comprised 40 *Dryopteris* accessions and three outgroup (*Arachniodes*) accessions (Appendix 1). Of the 43 plastomes analyzed, 20 were sourced from NCBI GenBank, and 23 were newly sequenced using silica-gel-dried leaf fragments collected in the field.

For each sample, total DNA was extracted from 15 mg of leaf fragments using the Magnetic Plant Genomic DNA Kit (Tiangen Biotech, Beijing). Libraries were constructed and sequenced (150-bp paired-end reads, >2 Gb per sample) on the MGI DNBSEQ-T7 platform by Anoroda Gene Technology Company (Beijing). Raw reads were assembled into plastomes using GetOrganelle v.1.7.7.0 (Jin et al. 2020), then circularized and annotated in Geneious 9.0.2 (Kearse et al. 2012) with the plastome of *D. rubrobrunnea* (Du et al. 2021) as the reference. These new plastomes and the 20 plastomes from GenBank were aligned with MAFFT v.7 (Katoh and Standley 2013), manually refined in Geneious v.9.0.2 (Kearse et al. 2012), and gap-trimmed using trimAl v.1.4 (Capella-Gutierrez et al. 2009).

The matrix containing 43 plastomes was analyzed using maximum likelihood (ML), maximum parsimony (MP), and Bayesian inference (BI). ML analysis was performed in IQ-TREE v.2.1.4 (Minh et al. 2020) with 10,000 ultrafast bootstrap (UFBoot) replicates to assess branch support. For MP analysis, PAUP* ver. 4.0a169 (Swofford 1991) was employed under equal character weighting, treating gaps as missing data; heuristic searches involved 1,000 replicates using tree bisection-reconnection (TBR) branch swapping, saving 100 trees per random sequence addition, and MP bootstrap values (MPBS) were calculated from 1,000 replicates. Bayesian inference was conducted as follows: the best substitution model was first selected via jModelTest 2.1.10 (Darriba et al. 2012), after which MrBayes 3.2.7 (Ronquist et al. 2012) executed four parallel Markov chain Monte Carlo (MCMC) chains for 10 million generations, sampling one tree every 1,000 generations. Bayesian posterior probabilities (BIPP) were derived from the 75% majority-rule consensus tree after discarding the initial 25% of samples as burn-in.

## Results

The morphological study showed that the specimens (*LXZ 16451*) from northern Vietnam share some key characters with specimens of *Dryopteris* sect. *Splendentes* from the Sino-Himalaya region: large bipinnate fronds, less copious scales on the basal stipe, broad scales on the rachis, linear-lanceolate and sessile (rarely very shortly petiolulate) pinnae, and oblong and mostly short-petiolulate pinnules. These are characters distinguishing sect. *Splendentes* from other groups of *Dryopteris* with non-bullate scales (*Dryopteris* subg. *Dryopteris* sensu Fraser-Jenkins). All these specimens exhibit two distinct states of pinnule dissection: lobate (or pinnatifid toward the base) occurring in *D. rubrobrunnea* and *D. splendens* (Fig. 1A, B), and pinnatisect occurring in *D. sikkimensis* and the specimens from northern Vietnam (Fig. 1C, D). Compared with the three other species, the specimens from northern Vietnam are unique in having very densely distributed, broad-lanceolate scales on the stipe (excluding the basal portion) and rachis (Fig. 1C), fibrillose scales on both surfaces of pinnules, and auriculate acroscopic bases of pinnae (Table 1). Our morphological

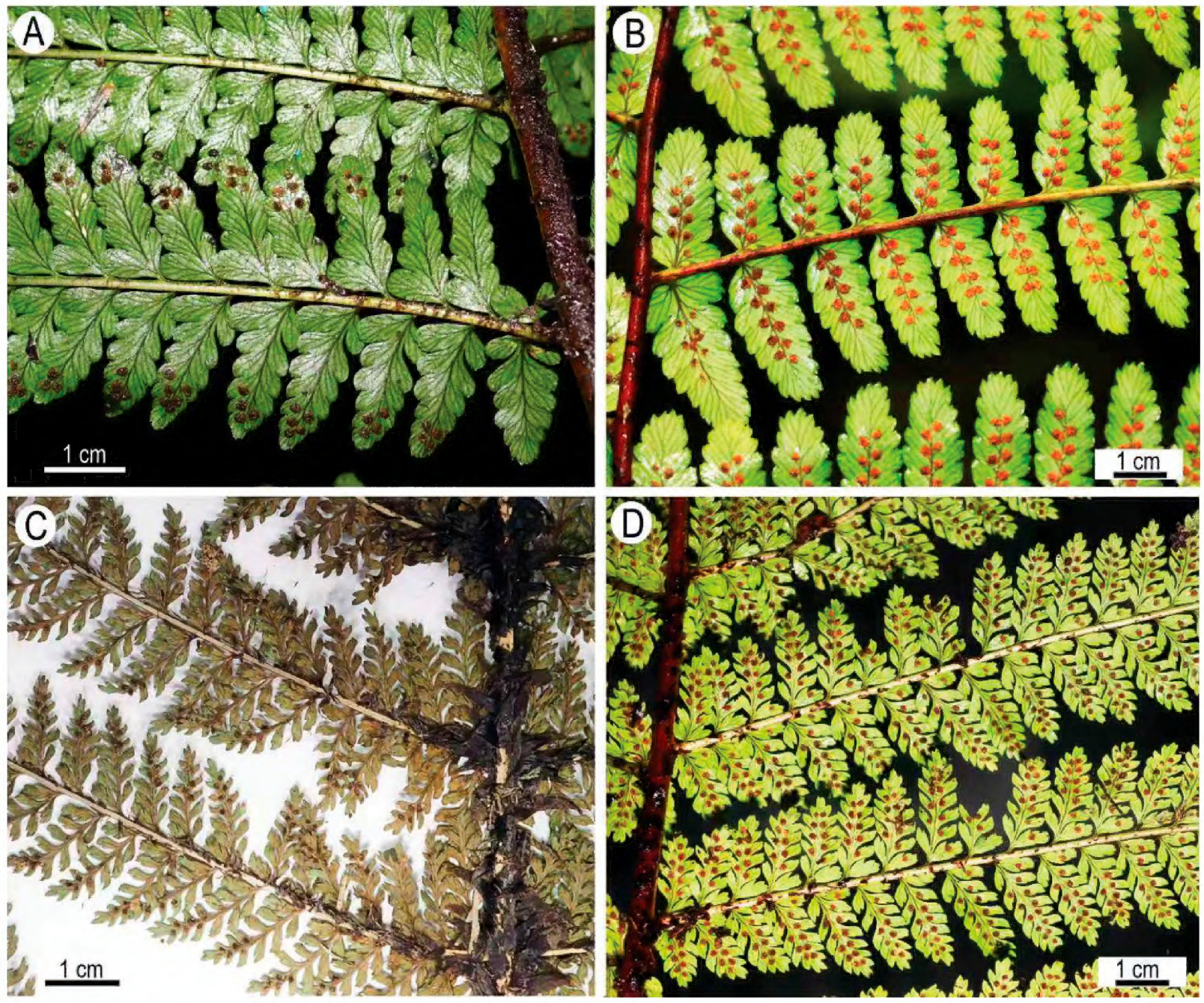


**Figure 1.** Morphological comparison of four species in *Dryopteris sect. Splendentes*. **A.** *D. rubrobrunnea* (*Zuo 7158*, KUN); **B.** *D. splendens* (*Zuo 2740*, KUN); **C.** *D. pycnolepis* (*Zhou 16451*, IBSC); **D.** *D. sikkimensis* (*Zuo 2565*, KUN).

**Table 1.** Morphological comparison of four species in *Dryopteris* sect. *Splendentes*.

| Character | *D. rubrobrunnea* | *D. splendens* | *D. pycnolepis* | *D. sikkimensis* |
|---|---|---|---|---|
| Color of stipe & rachis | Reddish brown or occasionally stramineous | **Atrocastaneous*** | Stramineous | Stramineous or occasionally reddish brown |
| Scale abundance on stipe & rachis | Sparse or somewhat dense | Sparse | **Very dense** | Sparse or sometimes dense |
| Large scale on stipe & rachis | Ovate or Ovate-lanceolate | Ovate-lanceolate | **Broadly lanceolate** | Ovate-lanceolate |
| Lamina texture | herbaceous | **Subcoriaceous** | herbaceous | herbaceous |
| Pinnule orientation | Ascending 60–80° to costa | **Patent or slightly reflexed** | Ascending 50–60° to costa | Ascending 50–70° to costa |
| Pinnule division | Lobate or pinnatifid toward base | Lobate or pinnatifid toward base | Pinnatisect | Pinnatisect |
| Basal pinnule on acroscopic costa | Equal in length to the next one | Equal in length to the next one | **Obviously longer than the next one** | Equal in length to the next one |
| Pinnule surface | Glabrous | Glabrous | **Scaly, scales fibrillose** | Glabrous |
| Fertile portion of pinnule | Distal half | **Whole length** (except apical portion) | Distal half | Whole length (frequently leaving basal 1–3 lobes sterile) |
| Sori number per pinnule | 2–4(5) pairs | 4–8 pairs | 2–3 pairs | 4–8 pairs |
| Sori position | **Medial or inframedial** | Costular | Close to costules | Close to costules |

*Terms in bold indicate a unique character state for the corresponding species.

observations indicate that the specimens (*LXZ 16451*) from northern Vietnam represent a distinct species, which we herein call *D. pycnolepis*.

In the resultant matrix of 43 plastomes, the aligned sequence length is 139,878 base pairs (bp), of which 23,447 (16.8%) are variable sites and 14,637 (10.5%) are parsimony-informative sites. The length of the most parsimonious tree is 38,029 steps, with a consistency index of 0.72, a retention index of 0.885, and a rescaled consistency index of 0.637. The log-likelihood score of the ML tree is −420,260.758.

Phylogenetic analyses using ML, MP, and BI produced identical tree topologies, with nearly all branching nodes receiving maximal support values (UF-Boot/MPBS = 100%, BIPP = 1.0). All ingroups (specimens of *Dryopteris*) were well resolved into six clades: Fragrantes, Nothoperanema, Acrorumohra, Erythrovariae, Yoroii, and *Dryopteris* (Fig. 2). The Fragrantes formed the most basal clade of the genus, being sister to all other *Dryopteris* species. The three clades – Nothoperanema, Acrorumohra, and Erythrovariae – formed a well-supported group, which was sister to the clades Yoroii and *Dryopteris*. The members of sect. *Splendentes*, including the new species *D. pycnolepis*, each represented by

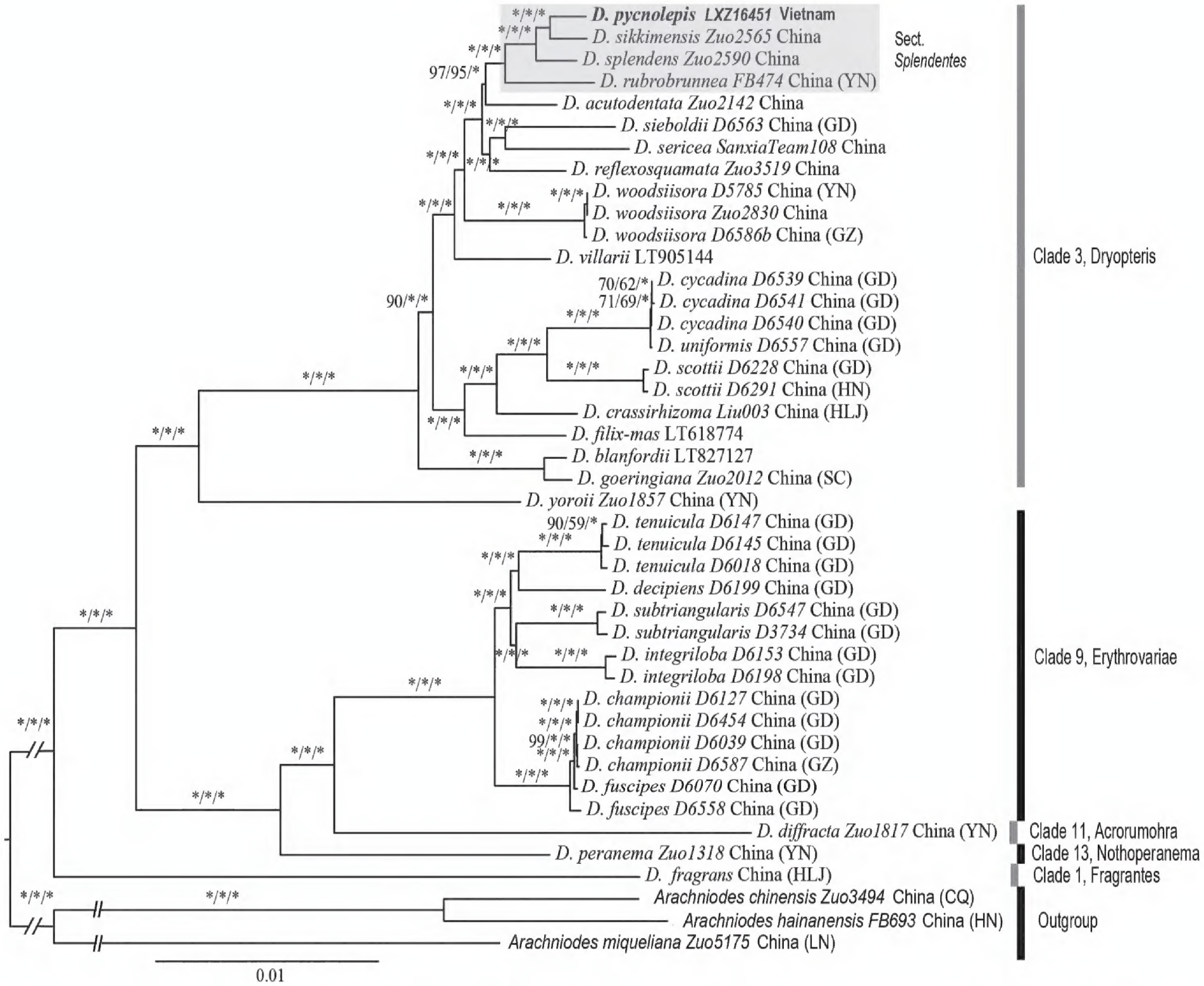
D. pycnolepis LXZ16451 Vietnam
D. sikkimensis Zuo2565 China
D. splendens Zuo2590 China
D. rubrobrunnea FB474 China (YN)
Sect. Splendentes
D. acutodentata Zuo2142 China
D. sieboldii D6563 China (GD)
D. sericea SanxiaTeam108 China
D. reflexosquamata Zuo3519 China
D. woodsiisora D5785 China (YN)
D. woodsiisora Zuo2830 China
D. woodsiisora D6586b China (GZ)
D. villarii LT905144
D. cycadina D6539 China (GD)
D. cycadina D6541 China (GD)
D. cycadina D6540 China (GD)
D. uniformis D6557 China (GD)
D. scottii D6228 China (GD)
D. scottii D6291 China (HN)
D. crassirhizoma Liu003 China (HLJ)
D. filix-mas LT618774
D. blanfordii LT827127
D. goeringiana Zuo2012 China (SC)
D. yoroii Zuo1857 China (YN)
D. tenuicula D6147 China (GD)
D. tenuicula D6145 China (GD)
D. tenuicula D6018 China (GD)
D. decipiens D6199 China (GD)
D. subtriangularis D6547 China (GD)
D. subtriangularis D3734 China (GD)
D. integriloba D6153 China (GD)
D. integriloba D6198 China (GD)
D. championii D6127 China (GD)
D. championii D6454 China (GD)
D. championii D6039 China (GD)
D. championii D6587 China (GZ)
D. fuscipes D6070 China (GD)
D. fuscipes D6558 China (GD)
D. diffracta Zuo1817 China (YN)
D. peranema Zuo1318 China (YN)
D. fragrans China (HLJ)
Arachniodes chinensis Zuo3494 China (CQ)
Arachniodes hainanensis FB693 China (HN)
Arachniodes miqueliana Zuo5175 China (LN)
Clade 3, Dryopteris
Clade 9, Erythrovariae
Clade 11, Acrorumohra
Clade 13, Nothoperanema
Clade 1, Fragrantes
Outgroup
0.01

**Figure 2.** Maximum likelihood phylogeny of selected species of *Dryopteris* based on plastome sequences. Five out of the 13 clades proposed by Zhang et al. (2012) and the previously unsampled Yoroii clade are annotated on the right. The position of sect. *Splendentes* (four accessions) is highlighted by a grey frame, with an arrow indicating the placement of the new species.

one accession, were resolved as a strongly supported monophyletic group within the *Dryopteris* clade, forming a sister relationship to *D. acutodentata* Ching. *Dryopteris acutodentata* is also an alpine forest species in the Sino-Himalaya region but differs morphologically from members of sect. *Splendentes* by its stipe base densely covered with lanceolate scales, 1-pinnate-pinnatifid lamina, and markedly short, triangular-lanceolate pinnae. Within sect. *Splendentes*, *D. rubrobrunnea* and *D. splendens* successively formed sister clades to the remaining species, with *D. pycnolepis* and *D. sikkimensis* constituting a terminal pair.

The comparison of plastome divergence between *D. pycnolepis* and *D. sikkimensis* with divergence among other conspecific accessions is presented in Table 2. The divergence between *D. pycnolepis* and *D. sikkimensis* measures 454 polymorphic sites (3.25‰ of total length), which is much higher than that observed in three species of the *Dryopteris* clade and four species of the Erythrovariae clade. Intraspecific plastome divergence across these examined accessions ranged from 1 to 111 sites (0.01–0.79‰ of plastome length).

## Discussion

Both morphological comparisons and phylogenetic analyses support that the specimens (*LXZ 16451*) from northern Vietnam represent a distinct species (*Dryopteris pycnolepis*). The markedly densely distributed scales on the stipe and rachis characterize *D. pycnolepis* (Figs 1C, 3B, C), clearly distinguishing this species from congeners with similar frond morphology. Additional diagnostic features separating *D. pycnolepis* from its closest relative, *D. sikkimensis*, include broadly lanceolate scales (versus ovate-lanceolate), the basal acroscopic pinnule longer than its adjacent pinnules (versus subequal), and fibrillose scales present on both surfaces of pinnules (versus glabrous). Morphological characters regarding scale shape and position on fronds, as well as the symmetry of the pinna base, are considered of taxonomic significance and thus are widely used in recognizing different sections within *Dryopteris* (Fraser-Jenkins 1986, 1989; Wu and Lu 2000; Wu et al. 2013). Phylogenetically, there is significant plastome divergence between accessions of *D. pycnolepis* and *D. sikkimensis*, evidenced by long branches in our phylogram (Fig. 2) and by divergence values much higher than observed intraspecific variations (Table 2), lending further

**Table 2.** Plastome divergence between *Dryopteris pycnolepis* and *D. sikkimensis* compared to intraspecific divergence within other *Dryopteris* species.

| Species name (accession numbers) | Systematic position | Sequence divergence (sites) | Permillage difference |
|---|---|---|---|
| *Dryopteris pycnolepis* (1)–*D. sikkimensis* (1) | *Dryopteris* clade | 454 | 3.25 |
| *Dryopteris woodsiisora* (3) | *Dryopteris* clade | 2–30 | 0.01–0.21 |
| *Dryopteris cycadina* (3) | *Dryopteris* clade | 3–17 | 0.02–0.12 |
| *Dryopteris scottii* (2) | *Dryopteris* clade | 58 | 0.41 |
| *Dryopteris tenuicula* (3) | *Erythrovariae* clade | 65–81 | 0.46–0.58 |
| *Dryopteris subtriangularis* (2) | *Erythrovariae* clade | 112 | 0.80 |
| *Dryopteris integriloba* (2) | *Erythrovariae* clade | 117 | 0.84 |
| *Dryopteris championii* (4) | *Erythrovariae* clade | 1–27 | 0.01–0.19 |
| *Dryopteris fuscipes* (2) | *Erythrovariae* clade | 111 | 0.79 |

support to the distinctness of *D. pycnolepis* as a separate species. Morphological and molecular evidence indicates that *D. pycnolepis* is possibly a replacement species of the Sino-Himalayan *D. sikkimensis* in northern Vietnam.

Both the morphological and phylogenetic studies support *D. pycnolepis*, *D. sikkimensis*, *D. rubrobrunnea*, and *D. splendens* as constituting a small natural group (sect. *Splendentes*) within *Dryopteris*. According to our observations on herbarium specimens and living plants, this section morphologically differs from other *Dryopteris* species or sections mainly in the less abundant scales on the basal portion of the stipe and the amply bipinnate lamina with sessile, linear-lanceolate pinnae. So far as we know, there are only these four species in sect. *Splendentes*. When establishing *Dryopteris* sect. *Splendentes*, Fraser-Jenkins (1986) assigned *D. bamleriana* Rosenst. (endemic to New Guinea), *D. kwanzanensis* Tagawa (endemic to Taiwan), and *D. reflexosquamata* Hayata (distributed from SW China to Taiwan) to this section along with species in the Sino-Himalaya region. All three species are clearly different from *D. pycnolepis* and other Sino-Himalayan members of sect. *Splendentes* by having much shorter pinnae (not linear-lanceolate). In addition, *D. bamleriana* differs in having obviously petiolulate pinnae (5–8 mm long), while both *D. kwanzanensis* and *D. reflexosquamata* differ by having the stipe base covered with abundant, reflexed scales. Phylogenetic analyses indicate that *D. reflexosquamata* and *D. kwanzanensis* are not members of sect. *Splendentes*. As shown in Fig. 2, the sampled *D. reflexosquamata* was resolved in a subclade with *D. sieboldii* and *D. sericea* within the *Dryopteris* clade, while *D. kwanzanensis* was demonstrated to be closely allied to *D. reflexosquamata* (Kuo et al. 2024). Thus, we conclude that *Dryopteris* sect. *Splendentes* is a small natural group restricted to the Sino-Himalaya region and northern Vietnam, currently comprising only four species with large-sized, bipinnate fronds, less abundant scales on the basal stipe, and sessile, linear-lanceolate pinnae.

Within *Dryopteris* sect. *Splendentes*, the interspecific relationships indicated by morphological comparison are not fully consistent with those suggested by plastome-based phylogenetic analyses. Except for the sister relationship between *D. pycnolepis* and *D. sikkimensis*, the relationships among *D. rubrobrunnea*, *D. splendens*, and the *D. pycnolepis*–*D. sikkimensis* clade differ between morphological and molecular evidence. Our morphological observations show that *D. rubrobrunnea* is very similar to *D. splendens*, both having nearly the same pattern of frond dissection (lobate or pinnatifid toward the base) (Figs 1A, B). *Dryopteris rubrobrunnea* (originally recorded as *D. rubripes* Ching & Chu, ined.) is morphologically intermediate between *D. splendens* and *D. sikkimensis* and is nearer to the former (Fraser-Jenkins 1989: 407, 408). Indeed, *D. splendens* possesses some unique characters, such as subcoriaceous lamina texture (versus herbaceous), patent or more-or-less reflexed pinnules (versus ascending), and sori borne on pinnules from the base to nearly the apex (versus restricted to the distal half of the pinnule) (Table 1), which make it the most distinct within sect. *Splendentes*. However, our phylogenetic analyses neither support the closest affinity of *D. rubrobrunnea* to *D. splendens* nor support that *D. rubrobrunnea* is closer to *D. splendens* than to the *D. pycnolepis*–*D. sikkimensis* clade (Fig. 2). The phylogenetic relationships indicating that *D. splendens* is closer to *D. pycnolepis* and *D. sikkimensis* than to *D. rubrobrunnea* are currently difficult to interpret morphologically. It must be acknowledged that the mor-

phology of species in sect. *Splendentes* remains insufficiently understood. For example, the spore morphology of *D. pycnolepis* appears unique (with smooth and glabrous perispores; Fig. 3F, G) when compared to the richly ornamented perispores in other species of *Dryopteris* (Tryon and Lugardon 1991; Wang and Dai 2010). However, the spore morphology of all species in sect. *Splendentes* (except *D. pycnolepis* described here) has not been documented, and spores of these species were unavailable for study. To better understand the morphology of this group, further field observations and the collection of complete fronds with rhizomes and mature spores are needed.

## Taxonomic treatment

***Dryopteris pycnolepis* Z.Y.Zuo & S.Y.Dong, sp. nov.**
urn:lsid:ipni.org:names:77369252-1
Figs 1C, 3, 4

**Type.** Vietnam • Lào Cai Province: Sa Pa District, Mt. Hoàng Liên; 22°18.47'N, 103°46.45'E; 17 June 2023; *L.X. Zhou 16451* (holotype, IBSC; isotypes: IBSC).

**Diagnosis.** *Dryopteris pycnolepis* is very similar to *D. sikkimensis* but differs in its stipe and rachis very densely covered with large scales (versus obviously sparse, scattered scales) and the pinnules abaxially with long, fibrillose scales (versus pinnules glabrous).

**Description.** ***Plants*** medium to large, 50–90 cm tall. ***Rhizome*** short, with fronds clustered on its apex; ***stipe*** 20–35 cm long (shorter than rachis), 2–3.5 mm thick, thickened at base (to 5 mm), lower portion (in basal 6–8 cm length from the base) dark brown, upwards stramineous, matte, together with rachis narrowly grooved adaxially and densely scaly except for the basal portion in dark brown (which bearing relatively few scales); ***scales*** dark brown or mostly blackish, lustrous, chartaceous, spreading acroscopically or laterally, polymorphic in size, smaller ones lanceolate, ca. 1.2 × 0.2 mm, larger ones or broadly lanceolate, 8–10 × 1.5–2.2 mm, apex acuminate or acute, base truncate or slightly cordate, margins entire or minutely erose; ***lamina*** herbaceous, adaxially dark green and abaxially pale green when living, oblong-lanceolate, 30–55 × 15–25 cm, bipinnate-pinnatisect, apex somewhat abruptly narrowed and acuminate, bearing 13–15 pairs of pinnae below the abruptly reduced terminal portion; ***rachis*** stramineous, densely scaly, with similar scales abaxially and linear or fibrillose scales (to 3–5 mm long) adaxially (the latter borne on rachis groove); ***pinnae*** linear or narrowly linear-lanceolate, spaced 5–8 mm apart except at base (where contiguous), subopposite or sometime those on upper rachis alternative, mostly patently spreading (with an approximately right anger to rachis) at base and distally curved toward frond apex, sessile, all pinnae (except those on terminal reduced portion of lamina) almost of the same size, with the lowest 1–2 pairs not or slightly shortened, middle pinnae 10–15 × 2–3 cm (with the widest base up to 4 cm wide), base asymmetrical, acroscopic base truncate (parallel to rachis and partly overlapping rachis), basiscopic base round or cuneate, apex acuminate, with copious, blackish, lanceolate scales on abaxial costae, the large pinna bearing 15–25 pairs of pinnules; ***pinnules*** generally alternative, obliquely spreading (forming an angle of ca. 50–60° to costa), nearly oblong, very shortly stalked, middle pinnules 1.8–2 cm long and 6–8 mm wide at base, acroscopic

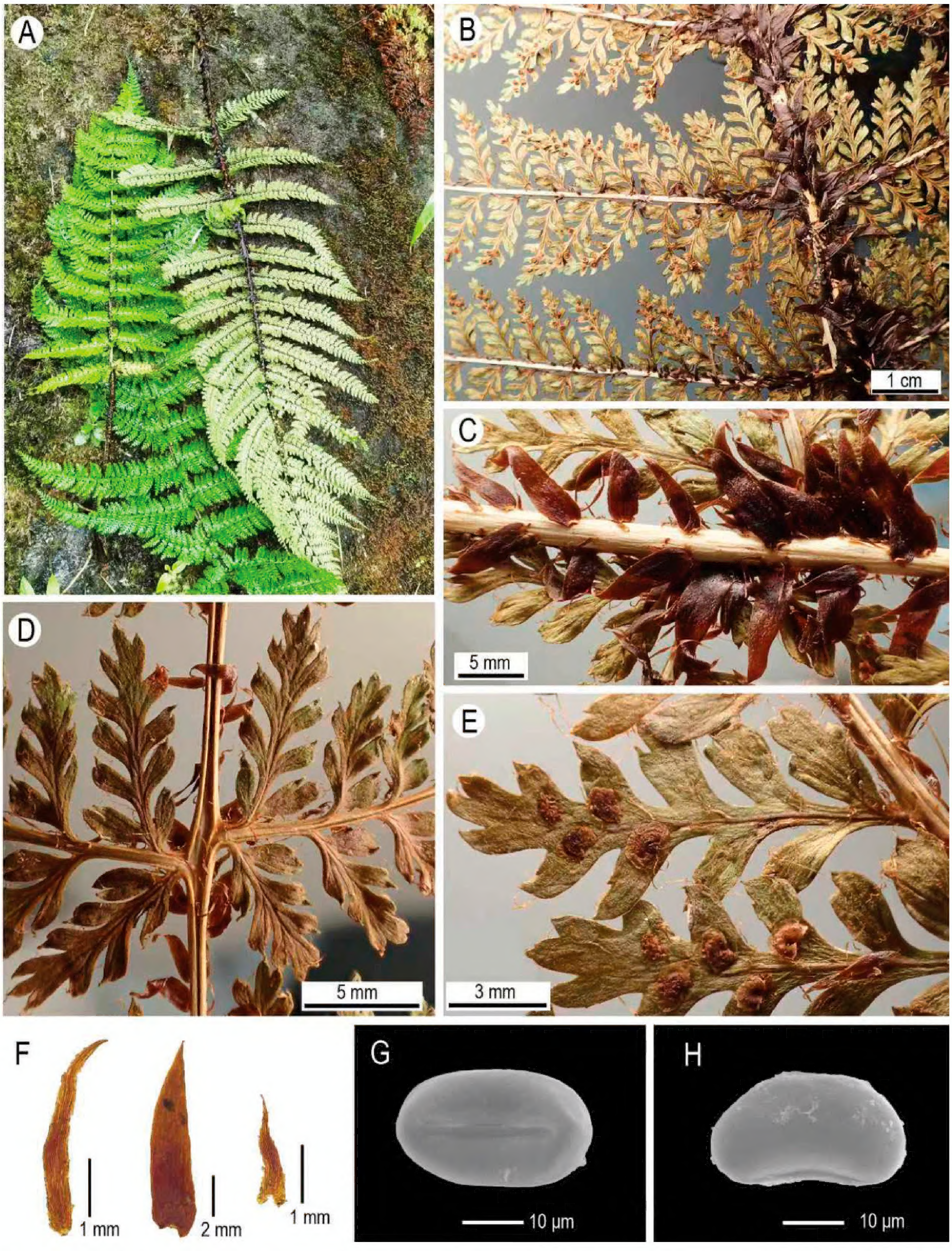


**Figure 3.** Morphology of *Dryopteris pycnolepis* Z.Y.Zuo & S.Y.Dong. **A.** Three fronds cut in the field; **B.** Three pairs of middle pinnae on rachis (abaxial view); **C.** Detail of rachis scales (abaxial view); **D.** Detail of a pair of upper pinnae (basal portions) on rachis (adaxial view); **E.** Detail of two pinnules on a pinna (abaxial view), showing fibrillose scales on pinnule surface and sori on distal half of pinnules; **F.** Scales on stipe; **G.** Proximal view of a spore; **H.** Lateral view of a spore. (All from *L.X.Zhou 16451* at IBSC).

**Figure 4.** Holotype of *Dryopteris pycnolepis* Z.Y.Zuo & S.Y.Dong (*L.X.Zhou 16451*, IBSC).

base truncate, basiscopic base round, apex obtuse, the acroscopic basal pinnule the longest (to 2.5 cm) and obviously longer than the second pinnule, pinnatisect, with fibrillose scales (ca. 5 mm long) on abaxial surfaces of costules and veins (fewer fibrillose scales present on adaxial surface); lobes of a middle pinnule 5–7 pairs, ascending, narrowly oblong, ca. 2.5–4.5 × 1.2–1.5 mm, apex round or obtuse, apiculate with 1–2 teeth, spaced ca. 1 mm apart; ***veins*** free, slightly visible on both surfaces, simple, once or twice forked, not reaching lamina margins. ***Sori*** round, confined to upper half of pinnules, 2–3 pairs per pinnule, one per segment, dorsal on the base of acroscopic veinlet, close to costules; ***indusia*** orbicular-reniform, large, ca. 1 mm in diameter, approximate to each other, margin entire, brown, membranous, persistent; ***spore*** reniform, monolete, ca. 32 × 16.5–18 μm, with smooth, glabrous surface of perispores.

**Habitat.** Terrestrial alongside a trail in montane broadleaved evergreen forest, elevation 2860 m; currently only a small population observed in Mt. Hoàng Liên, northern Vietnam.

**Etymology.** The specific epithet comes from the Latin words "*pycno-*"(densely bearing) and "*lepis*" (scales), referring to the scales densely borne on the stipe, and rachis.

***Dryopteris splendens* (Bedd.) Kuntze, Revis. Gen. Pl. 2: 813. 1891.**

*Nephrodium splendens* Hook.; Sp. Fil. [W.J.Hooker] 4: 126 (1862), nom. illeg., non *Nephrodium splendens* (Willd.) Desv. (1827); *Lastrea splendens* Bedd., Ferns Brit. India 1: t. 42. 1865, nom. nov. Type: INDIA. West Bengal, "Sikkim"; *J.D.Hooker s.n.* (lectotype, K, designated by Fraser-Jenkins in Bull. Brit. Mus. Nat. Hist., Bot. 18(5): 405. 1989, not seen; isolectotypes: B, barcode B200067565, B200067569, B200067570, B200067571; BR, barcode BR0000032264388, BR0000032264395; E, barcode E01467890, E01467891; GH, barcode 00021663; NY, barcode 04153316, 04153317; P, barcode P01603131, P01603132, P01603131; U barcode U.1009785; ZT, barcode ZT-00278799).

*Aspidium splendens* Willd., Sp. Pl., ed. 4 [Willdenow] 5: 220 (1810). *Nephrodium splendens* (Willd.) Desv., Mém. Soc. Linn. Paris 6(3): 253 (1827). Type: MAURITIUS. *Wallich list no. 2241* (holotype, K001115453) (Excluding).

**Note.** The correct authorship for *Dryopteris splendens* is "(Bedd.) Kuntze," not "(Hook.) Kuntze" as cited by many authors (e.g., Fraser-Jenkins 1986, 1989; Wu and Lu 2000; Wu et al. 2013; Fraser-Jenkins et al. 2018), nor "(Desv.) Kuntze" as shown in Hassler's (1994–2025) World Plants database. This taxon was originally described by Hooker (1862) as *Nephrodium splendens*. Hooker's name, however, is a later homonym of *Nephrodium splendens* (Willd.) Desv. (Desvaux 1827) and is therefore illegitimate. Consequently, it cannot serve as the basonym for subsequent combinations. The second earliest name of this taxon, *Lastrea splendens* Bedd., is legitimate under ICN Art. 6.5 and can be considered, under ICN Art. 6.13, a new name. Therefore, it can serve as the basonym for later combinations where necessary. Thus, the authorship of *Dryopteris splendens* proposed by Kuntze (1891) should be attributed to "(Bedd.) Kuntze."

## Acknowledgments

We are grateful to the curators and staff of the following herbaria for facilitating access to digitized specimens through their online databases: B, BR, C, CDBI, E, GH, H, K, KUN, L, MICH, MO, NY, P, PE, S, US, TENN, and ZT. LXZ thanks Dr. Vu Van Lien from the Vietnam National Museum of Nature for his kind help in obtaining the specimen collection permit for Hoàng Liên National Park.

## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

## Ethical statement

No ethical statement was reported.

## Use of AI

No use of AI was reported.

## Funding

This study was supported by the Guangdong S&T Program (grant no. 2022B1111230001) and the Bio-taxonomist Program of the Chinese Academy of Sciences (CAS-TAX-24 047).

## Author contributions

Conceptualization, SYD and ZYZ; methodology, SYD and JKH; formal analysis, SYD and JKH; investigation, SYD and LXZ; resources, LXZ; data curation, XJL and ZYZ; writing, SYD and JKH; visualization, SYD and JKH; funding acquisition, SYD.

## Author ORCIDs

Jun-Kai Huang https://orcid.org/0009-0003-1497-8173
Zheng-Yu Zuo https://orcid.org/0000-0002-8334-6132
Shi-Yong Dong https://orcid.org/0000-0002-8449-7856

## Data availability

All data are available within the paper. New nucleic acid sequences are being deposited in GenBank.

## References

Capella-Gutierrez S, Silla-Martinez JM, Gabaldon T (2009) trimAl: A tool for automated alignment trimming in large-scale phylogenetic analyses. Bioinformatics (Oxford, England) 25: 1972–1973. https://doi.org/10.1093/bioinformatics/btp348

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: More models, new heuristics and parallel computing. Nature Methods 9: 772–772. https://doi.org/10.1038/nmeth.2109

Desvaux NA (1827) Prodrome de la famille des fougères. Mémoires de la Société linnéenne de Paris 6(3): 171–337.

Du XY, Lu JM, Zhang LB, Wen J, Kuo LY, Mynssen CM, Schneider H, Li DZ (2021) Simultaneous diversification of Polypodiales and angiosperms in the Mesozoic. Cladistics 37: 518–539. https://doi.org/10.1111/cla.12457

Fraser-Jenkins CR (1986) A classification of the genus *Dryopteris* (Pteridophyta: Dryopteridaceae). Bulletin of the British Museum (Natural History). Botany 14: 183–218.

Fraser-Jenkins CR (1989) A monograph of *Dryopteris* (Pteridophyta: Dryopteridaceae) in the Indian subcontinent. Bulletin of the British Museum (Natural History). Botany 18: 323–477.

Fraser-Jenkins CR, Gandhi KN, Kholia BS (2018) An annotated checklist of Indian pteridophytes, part-2. Bishen Singh Mahendra Pal Singh, Dehra Dun, 1–573.

Hassler M (1994–2025) World Plants. Synonymic Checklist and Distribution of the World Flora. Version 25.06. www.worldplants.de [Last accessed 06/20/2025]

Hooker WJS (1862) Species filicum. vol. 4. W. Pamplin, London, 1–292.

Jin JJ, Yu WB, Yang JB, Song Y, dePamphilis CW, Yi TS, Li DZ (2020) GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. Genome Biology 21: 241. https://doi.org/10.1186/s13059-020-02154-5

Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. Molecular Biology and Evolution 30: 772–780. https://doi.org/10.1093/molbev/mst010

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: An integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics (Oxford, England) 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Kuntze O (1891) Revisio generum plantarum. vol. 2. A. Felix, Leipzig; U. Hoepli, Milano; Dulau & Co., London; G. E. Stechert, Newyork; C. Klincksieck, Paris, 375–1011.

Kuo LY, Chang YH, Glowienka JMO, Amoroso VB, Dong SY, Kao TT, Wang CN, Chiou WL (2016) A Revised Framework of *Dryopteris* subg. *Nothoperanema* (Dryopteridaceae) Inferred from Phylogenetic Evidence, with Descriptions of Two New Sections. Systematic Botany 41: 596–605. https://doi.org/10.1600/036364416X692334

Kuo LY, Tang SK, Huang YH, Xie PJ, Chen CW, Chang ZX, Hsu TC, Chang YH, Chao YS, Chen CW, Fawcett S, Nitta JH, Sundue M, Kao TT, Luu HT, Mustapeng AMA, Coritico FP, Amoroso VB, Thai YK (2024) A DNA barcode reference of Asian ferns with expert-identified voucher specimens and DNA samples. Scientific Data 11: 1314. https://doi.org/10.1038/s41597-024-04161-8

Minh BQ, Schmidt HA, Chernomor O, Schrempf D, Woodhams MD, von Haeseler A, Lanfear R (2020) IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. Molecular Biology and Evolution 37: 1530–1534. https://doi.org/10.1093/molbev/msaa131

PPG I (2016) A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 54: 563–603. https://doi.org/10.1111/jse.12229

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Swofford DL (1991) PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1 Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Tryon AF, Lugardon B (1991) Spores of the Pteridophyta. Springer-Verlag, New York, 1–548.

Wang QX, Dai XL (2010) Spores of Polypodiales(Filicales) from China. Science Press, Beijing, 1–259.

Wu SK, Lu SG (2000) *Dryopteris* subg. *Dryopteris*. In: Wu SK (Ed.) Flora Republica Popularis Sinicae, *Vol. 5* (*1*). Science Press, Beijing, 102–220.

Wu SK, Xiang JY, Barrington DS (2013) *Dryopteris*. In: Wu ZY, Raven PH, Hong DY (Eds) Flora of China, vols. 2–3. Science Press, Beijing; Missouri Botanical Garden Press, St. Louis, 571–628.

Zhang LB, Zhang L (2012) The inclusion of *Acrophorus*, *Diacalpe*, *Nothoperanema*, and *Peranema* in *Dryopteris*: The molecular phylogeny, systematics, and nomenclature of *Dryopteris* subg. *Nothoperanema* (Dryopteridaceae). Taxon 61: 1199–1216. https://doi.org/10.1002/tax.616003

Zhang LB, Zhang L, Dong SY, Sessa EB, Gao XF, Ebihara A (2012) Molecular circumscription and major evolutionary lineages of the fern genus Dryopteris (Dryopteridaceae). BMC Evolutionary Biology 12. https://doi.org/10.1186/1471-2148-12-180

Zuo ZY, Rouhan G, Dong SY, Liu HM, Du XY, Zhang LB, Lu JM (2025) A revised classification of Dryopteridaceae based on plastome phylogenomics and morphological evidence, with the description of a new genus, *Pseudarachniodes.* Plant Diversity 47: 34–52. https://doi.org/10.1016/j.pld.2024.07.010

## Appendix 1

Accessions were used for phylogenetic analyses in this study. Information is arranged in this order: species name, voucher specimen (collector, number, and herbarium), place of origin, and GenBank number of plastome. The dash (–) indicates information not available; the asterisk (*) indicates sequences newly generated in this study.

***Arachniodes chinensis*** (Rosenst.) Ching, *Z.Y. Zuo 3494* (KUN), China (Chongqing), OR530038. ***Arachniodes hainanensis*** (Ching) Ching, *Q. Wei et al. FB693* (KUN), China (Hainan), MT130572. ***Arachniodes miqueliana*** (Maxim. ex Franch. & Sav.) Ohwi, *Z.Y. Zuo 5175* (KUN), China (Liaoning), OR530039. ***Dryopteris acutodentata*** Ching, *Z.Y. Zuo 2142* (KUN), China (Yunnan), OQ649801. ***Dryopteris blanfordii*** (C. Hope) C. Chr., –, Russia (in cult.), LT827127. ***Dryopteris championii*** (Benth.) C.Chr. ex Ching, *S.Y. Dong 6039* (IBSC), China (Guangdong), PV868338*; *S.Y. Dong 6127* (IBSC), China (Guangdong), PV868339*; *S.Y. Dong 6454* (IBSC), China (Guangdong), PV868340*; *S.Y. Dong 6526* (IBSC), China (Guangdong), PV868341*. ***Dryopteris crassirhizoma*** Nakai, *LiuBD003* (KUN), China (Heilongjiang), MT130689. ***Dryopteris cycadina*** (Franch. & Sav.) C. Chr., *S.Y. Dong 6539* (IBSC), China (Guangdong), PV868342*; *S.Y. Dong 6540* (IBSC), China (Guangdong), PV868343*; *S.Y. Dong 6541* (IBSC), China (Guangdong), PV868344*. ***Dryopteris decipiens*** (Hook.) Kuntze, *7333* (PE), China (Guizhou), KY427348. ***Dryopteris diffracta*** (Baker) C. Chr., *Z.Y. Zuo 1817*(KUN), China (Yunnan), OQ649848. ***Dryopteris filix-mas*** (L.) Schott, –, Russia (in cult.), LT618774. ***Dryopteris fragrans*** (L.) Schott, –, China (Heilongjiang), KX418656. ***Dryopteris fuscipes*** C. Chr., *S.Y. Dong 6070* (IBSC), China (Guangdong), PV868345*; *S.Y. Dong 6558* (IBSC), China (Guangdong), PV868346*. ***Dryopteris goeringiana*** (Kunze) Koidz., *Z.Y. Zuo 2012* (KUN), China (Sichuan), OQ649863. ***Dryopteris integriloba*** C. Chr., *S.Y. Dong 6153* (IBSC), China (Guangdong), PV868347*; *S.Y. Dong 6198* (IBSC), China (Guangdong), PV868348*. ***Dryopteris peranema*** Li Bing Zhang, *Z.Y. Zuo 1318* (KUN), China (Yunnan), OQ649938. ***Dryopteris pycnolepis*** Z.Y.Zuo & S.Y.Dong, *L.X. Zhou 16451* (IBSC), Vietnam, PV868360*. ***Dryopteris reflexosquamata*** Hayata, *Z.Y. Zuo 3519* (KUN), China (Guizhou), OQ649953. ***Dryopteris rubrobrunnea*** W. M. Chu, *Cheng X. et al. FB474* (KUN), China (Yunnan), MT130582. ***Dryopteris scottii*** (Bedd.) Ching, *S.Y. Dong 6228* (IBSC), China (Guangdong), PV868349*; *S.Y. Dong 6291* (IBSC), China (Hainan), PV868350*. ***Dryopteris sericea*** C. Chr., *SanxiaTeam 108* (PE), China (Chongqing), OQ649963. ***Dryopteris sieboldii*** (T. Moore) Kuntze, *S.Y. Dong 6563* (IBSC) China (Hainan), PV868351*. ***Dryopteris sikkimensis*** (Bedd.) Kuntze, *Z.Y. Zuo 2565* (KUN), China (Xizang), OQ649967. ***Dryopteris splendens*** (Hook.) Kuntze, *Z.Y. Zuo 2590* (KUN), China (Xizang), OQ649972. ***Dryopteris subtriangularis*** (C. Hope) C. Chr.,

*S.Y. Dong 3734* (IBSC), China (Guangdong), PV868352*; *S.Y. Dong 6547* (IBSC), China (Guangdong), PV868353*. ***Dryopteris tenuicula*** Matthew & Christ, *S.Y. Dong 6018* (IBSC), China (Guangdong), PV868354*; *S.Y. Dong 6145* (IBSC), China (Guangdong), PV868355*; *S.Y. Dong 6147* (IBSC), China (Guangdong), PV868356*. ***Dryopteris uniformis*** Makino, *S.Y. Dong 6557* (IBSC), China (Guangdong), PV868357*. ***Dryopteris villarii*** (Bellardi) Woyn. ex Schinz & Thell., –, Russia (in cult.), LT905144. ***Dryopteris woodsiisora*** Hayata, *Z.Y. Zuo 2830* (KUN), China (Yunnan), OQ649996; *S.Y. Dong 5785* (IBSC), China (Yunnan), PV868358*; *S.Y. Dong 6586b* (IBSC), China (Guizhou), PV868359*. ***Dryopteris yoroii*** Seriz., *Z.Y. Zuo 1857* (KUN), China (Yunnan), MW796579.